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Single Neurons in Posterior Parietal Cortex of Monkeys Encode Cognitive Set

Gijsbert Stoet* and Lawrence H. Snyder
Washington University in St. Louis
School of Medicine
Department of Anatomy and Neurobiology
660 South Euclid Avenue
St. Louis, Missouri 63110

Summary

The primate posterior parietal cortex (PPC), part of the dorsal visual pathway, is best known for its role in encoding salient spatial information. Yet there are indications that neural activity in the PPC can also be modulated by nonspatial task-related information. In this study, we tested whether neurons in the PPC encode signals related to cognitive set, that is, the preparation to perform a particular task. Cognitive set has previously been associated with the frontal cortex but not the PPC. In this study, monkeys performed a cognitive set shifting paradigm in which they were cued in advance to apply one of two different task rules to the subsequent stimulus on every trial. Here we show that a subset of neurons in the PPC, concentrated in the lateral bank of the intraparietal sulcus and on the angular gyrus, responds selectively to cues for different task rules.

Introduction

We can respond to the same stimulus in many different ways, depending on our current task state. Often, we know the task that we are performing well before a relevant stimulus appears. In this case, we can prepare our task in advance (Stoet and Snyder, 2003b). We define cognitive set as an abstract signal related to task preparation. This definition includes, for example, signals that either set or reflect selective attention to a particular dimension of a *forthcoming* stimulus. A cognitive set signal does not necessarily include details of how the task is to be performed.

Neuroimaging and neurophysiological studies in animals have shown that frontal cortex plays an essential role in supporting cognitive set (White and Wise, 1999; Asaad et al., 2000; Nakahara et al., 2002; Tanji and Hoshi, 2001; Wallis et al., 2001; Wallis and Miller, 2003). However, recent work suggests a role for the PPC in the flexible mapping of stimulus-response sets (Assad, 2003), although the idea that neurons in PPC might encode cognitive set independently of stimuli and responses has not yet been tested.

To address this issue, we trained macaque monkeys in a task-switching paradigm in which subjects rapidly alternate between two different stimulus-response mappings. Task-switching paradigms are optimally suited to the study of cognitive set (Rogers and Monsell, 1995; Meiran, 1996). When the task changes, the stimulus-response associations are changed, but the same sets of stimuli and the same sets of responses are used. In this way, brain activity related to cognitive set can be distinguished from activity encoding stimuli and responses.

Animals performed randomly interleaved trials of two different tasks. Each trial began with a visual task cue (yellow or blue screen color) that prompted one of two task rules. Each task rule specified what feature of an upcoming stimulus should be attended to and how to respond to that feature (Figure 1). The *color rule* required the animals to press the left button if the color of the upcoming stimulus was close to red and to press the right button if it was close to green. The *orientation rule* was to press the left button if the upcoming stimulus was close to vertical and the right button if the stimulus was close to horizontal (see Experimental Procedures for details, including differences in the tasks between the two animals). A delay period (190–485 ms) ensued, followed by a stimulus which required an immediate response. The stimulus was chosen from the identical set of 104 possible stimuli in both tasks. A given stimulus could instruct either the same or different button presses in the two tasks. As a result, information about both the stimulus and task rule was required in order to solve the task. Importantly, during the delay period, the animals had no information other than which of the two tasks to perform. Therefore, this paradigm is helpful in assessing the neural modulation correlated with cognitive set, independent of spatial attention, stimulus encoding, or motor planning.

To determine whether the activity of neurons in PPC reflects preparation for the upcoming task (cognitive set), we first asked whether the firing rates of PPC neurons were selectively modulated by the task rule during the delay period.

Results

We recorded from 378 isolated neurons in and around the intraparietal sulcus (IPS) of the right PPC of two animals (Figure 2). Task rule-selective neurons were identified by comparing the final 150 or 250 ms of delay period activity in trials starting with *yellow* versus *blue* task cues (Student's t tests). Twenty-nine percent of neurons ($n = 111$) showed a significant difference in activity and were therefore task rule selective by this measure (Figure 3).

We performed an additional Monte Carlo analysis to confirm the significance of this finding. Trials were randomly assigned to one task type or the other and then, using the same analysis as just described, the number of cells showing significant differences were tallied. We repeated this analysis 3000 times and never found more than 33 significant cells. Thus, the odds of obtaining our results (111 significant cells) by chance are less than $p = 0.00034$.

Most of the task rule-selective neurons were found in the lateral bank of the IPS and on the adjacent gyral

*Correspondence: stoet@pcg.wustl.edu

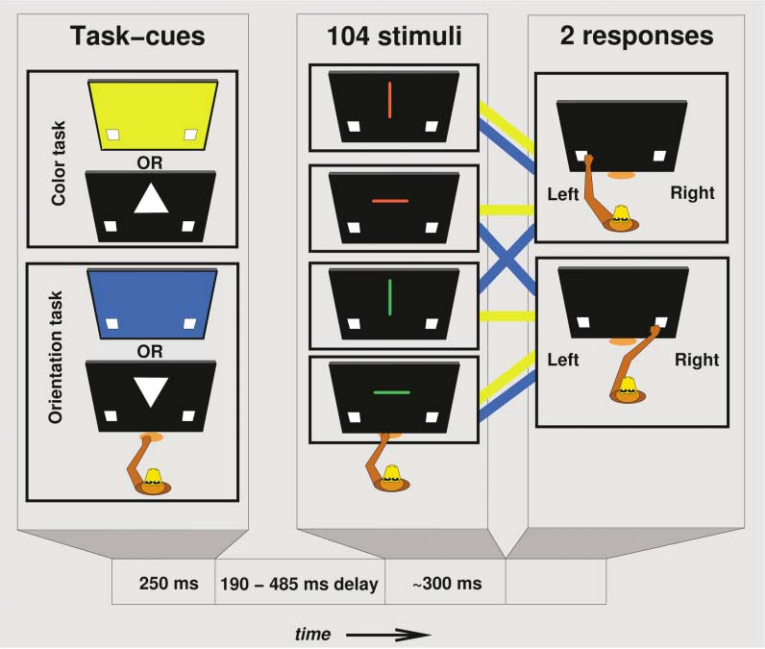

Figure 1. Experimental Paradigm

Each trial started with a 250 ms task cue indicating which of two task rules to apply to the subsequent stimulus. For each task rule, two different types of cues were used (a color or a shape) to distinguish between sensory and cognitive effects of the cues. After a 190–485 ms delay period, the stimulus, a colored oriented bar, appeared. Depending on the task rule, either the color or the orientation of the stimulus was relevant. In the color discrimination task, red stimuli required a left button press, and green stimuli required a right button press. In the orientation discrimination task, vertical bars required a left response, and horizontal bars required a right response. These stimulus-response mappings are indicated by yellow (color task) and blue (orientation task) lines between the four prototypical stimuli and the response alternatives. Variations in bar color (e.g., orange) and orientation (e.g., 10° from vertical) created a set of 104 stimuli. The stimulus disappeared once the animal lifted its paw off the home key (~300 ms reaction time). Liquid rewards followed correct responses.

surface (including areas LIPd, LIPv, 7a, LOP, and DP). Taking into account the fact that these areas were more densely sampled than more medial areas (i.e., the IPS fundus, medial wall, and area 5), the frequency of task rule-selective cells was more than twice as high in the lateral areas (35%, n = 95 out of 274) compared to the medial areas (15%, n = 16 out of 104, χ^2 test, $p < 0.001$). Similar numbers of neurons preferred one task rule or the other, and there was no statistically significant clustering of neurons preferring a single task within particular areas (tested by comparing proportions of cells of each rule type per area with χ^2 tests). Visual inspection of Figure 2 suggests a clustering of color task rule-selective cells in monkey 2 in areas 7a, DP, LIPd, and LIPv, but this did not reach statistical significance and was not replicated in monkey 1.

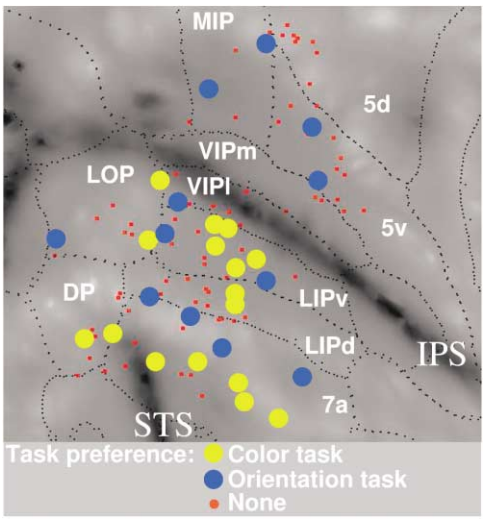

Figure 2. Map of Flattened Cortex

Shown are the recording sites in monkey 2, derived from a magnetic resonance image that was processed using the software packages Caret and SureFit (Van Essen et al. (2001), http://brainmap.wustl.edu/caret). Broad black lines indicate fundi of sulci. The top of the panel is medial and anterior; the bottom of the panel is lateral and posterior. Yellow and blue dots indicate locations of cells that fire preferentially in connection with color or orientation rules, respectively. Small red dots indicate recording locations of the remaining cells. Areal boundaries, though drawn as sharp lines, reflect the maximum likelihood based on a probability map and are therefore only approximate (Lewis and Van Essen (2000), http://brainmap.wustl.edu:8081/sums/archivelist.do?archive id=568272).

Consistent with other studies of parietal neurons emphasizing spatial responses (e.g., Leinonen et al., 1980; Robinson and Goldberg, 1978), many of the task rule-selective cells were spatially tuned, with 36% preferring contralateral responses and 17% preferring ipsilateral responses (Figure 3). In one animal, spatial tuning was significantly stronger when the preferred compared to the nonpreferred task was performed, but this effect was not replicated in the second animal.

We have shown elsewhere that monkeys prepare the upcoming task during the delay period (Stoet and Snyder, 2003b). It is possible that differences in task difficulty could produce differences in activity between the two task conditions that do not directly reflect cognitive set. This interpretation is ruled out by the finding of neurons selective for either rule. It is possible, however, that the animals "concentrated" on one task or the other, shifting their focus from session to session. To test for an influence of shifting behavioral strategies on the appearance of task cells, we correlated the magnitude of the task effect (firing during preparation for task 1 minus firing during preparation for task 2) with RT (RT for task 1 minus RT for task 2). We found no correlation (Pearson $R = 0.02$, $p > 0.7$) and concluded that fluctuating behavioral strategies do not account for the observed cell preferences.

A difference in firing in the two task rule conditions

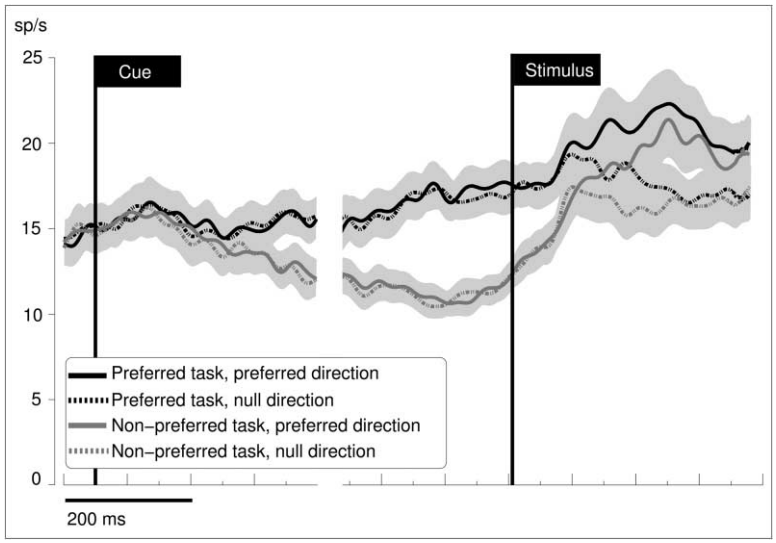

Figure 3. Time Course of the Average Activity of Task Rule-Selective Cells in PPC

Data are aligned on cue onset (left) or stimulus onset (right). For each of the 111 cells, we determined whether it preferred the color or orientation task. If the spike rate late in the delay period was significantly different in the two task conditions, then we defined the task condition with the higher spike rate as the preferred condition (Student's t test, α level of 0.05). We used the same preferred task assignment for both alignment intervals. We next determined the preferred direction during response selection for each cell and then sorted trials by task and direction. Traces show average activity, ± 1 SEM, during preferred (black) and nonpreferred (gray) tasks. This figure contains data only from those cells that show a significant effect of task and is intended to show the time course of the effect, not the existence or magnitude of the effect itself. On average, cells differentiated between preferred and nonpreferred task conditions 203 ms after cue onset and between left and right responses 92 and 104 ms after stimulus onset in the preferred and nonpreferred task conditions, respectively (see Experimental Procedures).

could reflect a difference in preparation for the upcoming task, but it could also reflect a difference in the sensory features of the two cues (i.e., yellow versus blue). To distinguish between these two possibilities, we performed an additional experiment to determine whether task rule selectivity was independent of the way in which the animals were instructed. We tested 192 neurons in two monkeys using either a color (yellow or blue) or a shape (upright or inverted triangles) to cue the task rule (Figure 1). Figure 4 shows two examples of task rule-selective cells in area 7a tested with this design. Four hundred milliseconds after cue onset, firing became markedly larger for orientation task trials compared to color task trials. This was true whether the task rule was conveyed by a color cue or by a shape cue. Rule-selective activity differences were slow to develop but were maintained throughout the remainder of the delay period. In one of the two cells (lower panel), this difference persisted for more than 300 ms after the stimulus appeared.

To determine whether neural responses during the delay period were different in the two task rule conditions, we applied a 2×2 analysis of variance (ANOVA) with the factors task rule (color discrimination or orientation discrimination) and task instruction cue set (colors or shapes) to each cell's neuronal responses during the late delay period. We found that 32% of neurons (42 out of 132) in the lateral wall of the IPS and the adjacent gyral surface had a main effect of task rule (Figure 5), which is similar to the percentage of neurons tested with one cue set. Of these, two-thirds ($n = 29$) showed a main effect of task rule without an interaction with task instruction cue set (colors versus shapes). This indicates that most task rule-selective neurons reflect the task rule independent from the way in which that rule was instructed. Outside of these regions (i.e., in the IPS fundus, medial wall, and in area 5), we saw similar albeit weaker effects: only 20% of neurons showed a main effect of task rule, and in over half, there was an interaction between task rule and task instruction cue set. Not surprisingly, main effects of task instruction cue set were common. Half of all PPC neurons tested in the lateral areas (62 of 132) responded differently to shape cues than to color cues. These main effects of cue set and the interactions between cue set and task reflect a strong influence of the sensory properties of the cue. This influence does not negate or diminish the slightly less prevalent effects of task on these neurons.

We examined the magnitude of the task effect using a receiver operating characteristic (ROC) analysis (Metz, 1978). For cells in the lateral wall of the IPS and the adjacent gyral surface, the area under the ROC curve was greater than 0.60 or less than 0.40 for 28.5% of cells (Figure 6A). For cells in more medial areas, this percentage was only 13.5%. Thus, not only was the number of statistically significant cells (shown in black) greater in the lateral areas, but the magnitude of the effects was also larger.

The time course of the mean ROC area is shown for both sets of areas in Figure 6B. Compared to the effect in the medial areas, task effects in the lateral areas begin sooner, are stronger, and are sustained well after the stimulus presentation. In contrast, the encoding of task information in the more medial areas starts later, is weaker, and is prominent only during the delay interval itself.

We next directly compared the pattern of task-selective activity in three different intervals: the immediate postcue period, the late delay period, and the immediate poststimulus period. To determine how sensitivity to sensory features is related to the encoding of the task, we applied an ROC analysis to activity recorded 50–150 ms after cue onset. Next, we assayed task selectivity by applying an ROC analysis to activity recorded in the late delay period. For each cell, we used the task instruction cue set to which the cell was most sensitive. We found no correlation between early cue selectivity and late task selectivity (Pearson $R = 0.05$, $p > 0.7$, Figure 7A) and conclude that there is no systematic relationship between selectivity to sensory features of the cue and task selectivity during the late delay period.

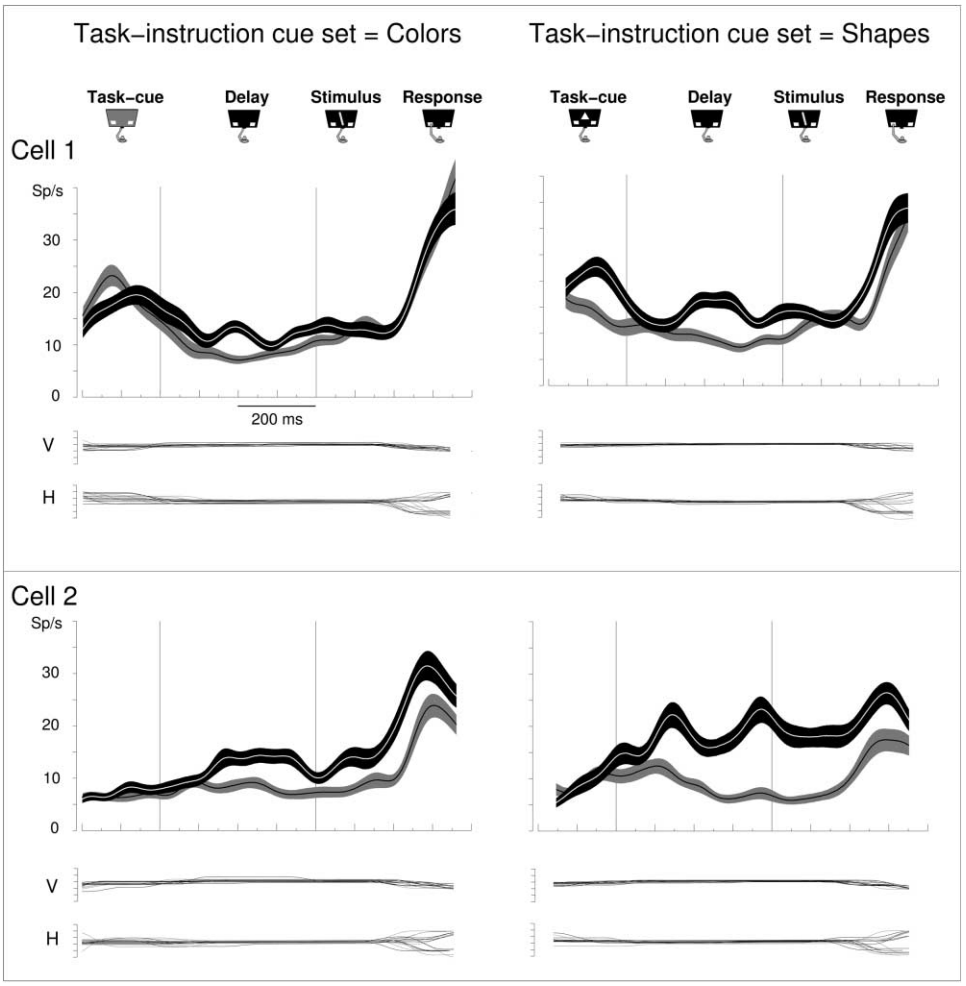

Figure 4. Examples of Two Task Rule-Selective Cells in Area 7a

Thick black and gray traces represent neuronal responses (mean ± 1 SEM) to color cues (left) and shape cues (right) instructing color and orientation task, respectively. Thin lines show the horizontal (H) and vertical (V) eye position. Tick marks on the ordinate of the eye trace plots correspond to 5° of visual angle. The upper two panels show a cell (364 trials) preferring the orientation task. Delay activity was consistently higher for orientation task trials irrespective of task instruction cue set. The lower two panels show a cell (384 trials) with a main effect of task as well as an interaction between task and cue. The interaction is evident in the larger task-selective response in the bottom right panel.

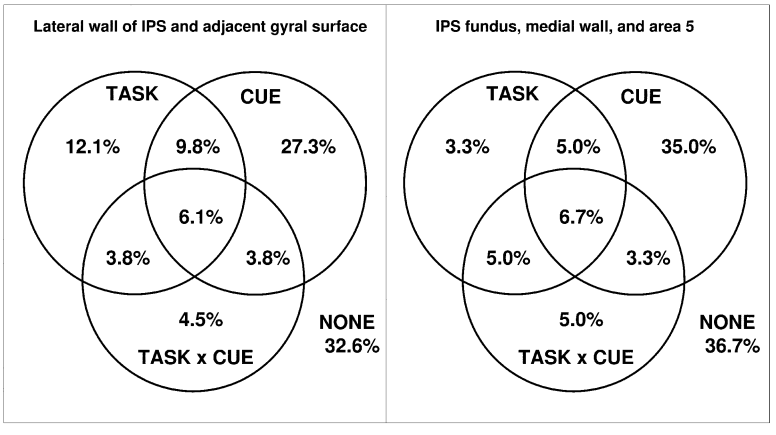

Figure 5. Venn Diagrams of the Results of the Analysis of Variance

An analysis of variance with the factors task and cue was applied to each of the 192 cells in two monkeys. The results are split up into cells recorded from the more lateral areas (left panel: lateral IPS and adjacent gyral surface) and cells recorded from the more medial areas (right panel: IPS fundus, medial wall, and area 5). In each Venn diagram, the three circles represent the main effects of "task," "cue," and the interaction term, respectively. For example, the 12.1% in the task circle means that 12.1% of cells had a main effect of task without a cue effect and with no interaction between task and cue. The number 9.8% in the overlapping task and cue circles means that 9.8% of cells had a main effect of task and a main effect of cue, but no interaction between task and cue. The α level used for each ANOVA was 0.05, so by chance we would expect that all main effects and interactions would sum to 5% in each of the two Venn diagrams.

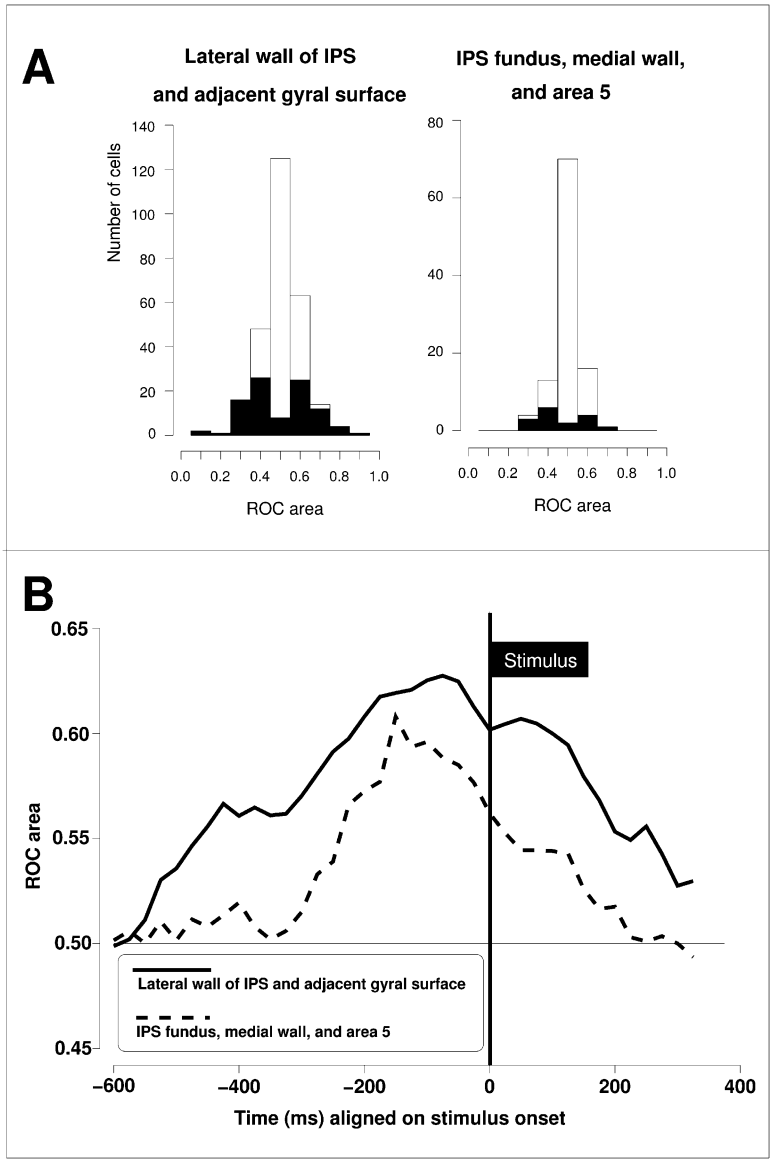

Figure 6. Distribution of Task Selectivity Index

(A) ROC analysis for activity recorded from cells in the lateral wall of IPS and the adjacent gyral surface (including areas LIPd, LIPv, 7a, LOP, and DP; left panel), and for cells in the IPS fundus, medial wall, and area 5 (right panel). Data are taken from the last 250 ms of the delay period. Cells with significant main effects of task in the ANOVA analysis (Figure 5) are indicated in black. The symmetrical nature of the distributions reflects the finding of equal numbers of cells selective for each of the two tasks.

(B) The time course of ROC values for significant task cells shows that task-selective activity in the lateral IPS and adjacent gyral surface (solid trace) starts earlier, reaches a higher value, and is maintained for longer than task-selective activity in the IPS fundus, medial wall, and area 5 (dashed trace).

To determine how task selectivity is affected by the presentation of the stimulus, we compared task selectivity immediately before and after stimulus presentation. Task encoding was very similar among cells in the lateral bank of the IPS and adjacent gyral surface: 27% of these neurons showed a main effect of task rule in the poststimulus period compared to 29% in the late delay period. An ROC analysis showed a strong correlation between task selectivity in these two intervals (Figure 7B, Pearson $R = 0.61$, $p < 0.0001$). Thus, task selectivity continues to be manifest even after the stimulus appears. However, unlike the responses measured in the cue stimulus interval, task-selective responses measured after the stimulus is presented may be contaminated by differential response preparation or differential response execution. For example, we often observed faster responses in one task compared to the other (Stoet and Snyder, 2003b), and such differences may have neural correlates in the parietal cortex. The advantage of the cue-stimulus design is that these confounds are not present during the cue-stimulus interval, and we therefore focus on this interval in this paper.

We have demonstrated that many neurons in PPC reflect information about the task and that many cells reflect cue information. We next asked whether task information could be extracted from the population of recorded neurons in a single trial. To test this, we used a very simple artificial neural network. A linear estimator was constructed using a two-layer network (Ben Hamed et al., 2003). Each input node (layer 1) corresponded to a particular neuron from our sample of recorded neurons and was assigned an activity equal to the firing rate of the corresponding neuron on a randomly selected trial. The network output (layer 2) was determined by a weighted sum of the activity of all the input nodes. The network was trained by adjusting the weights between the input nodes and the output node (see Experimental Procedures). An output activity greater than a criterion value indicated one task rule, while an output activity less than the criterion indicated the other task rule.

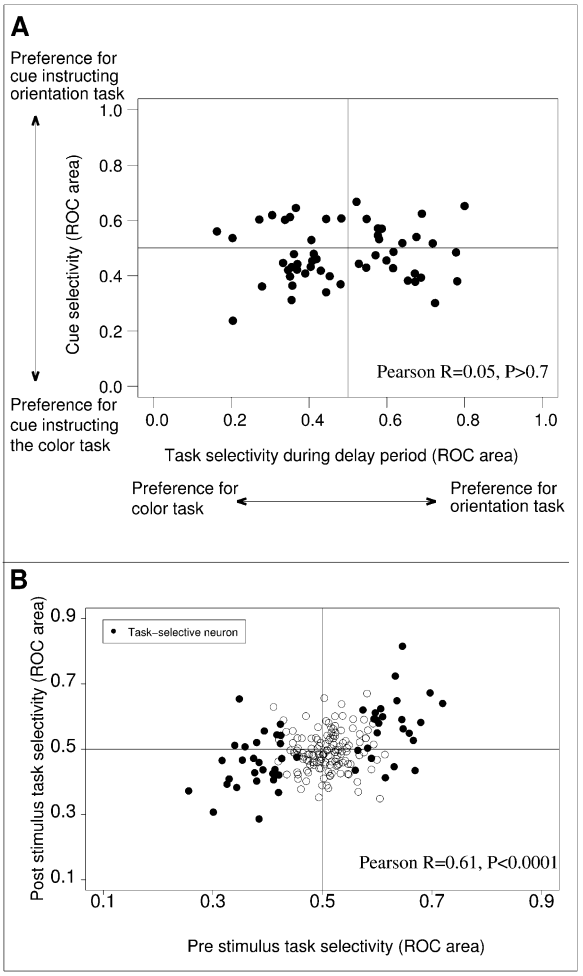

Figure 7. Comparison of Task Selectivity in Different Time Periods

(A) Cue sensitivity versus task sensitivity. Cue sensitivity is determined by calculating two ROC areas for the neural response to task cues (yellow versus blue color cues and upright versus inverted triangular shape cues). The larger of these two areas was then plotted against the ROC value for task selectivity. Cue sensitivity was measured in the interval 50–150 ms after the cue onset. Task sensitivity was measured in the late delay period. There was no significant correlation between cue and task responses ($p > 0.7$).

(B) Task selectivity in the prestimulus delay period and the poststimulus period. Task selectivity is determined by calculating ROC areas for the two task conditions in the prestimulus period (250 ms before stimulus onset) and in the poststimulus period (50–300 ms after the stimulus onset). There was a significant correlation between these two measures when calculated for task-selective neurons (Pearson $R = 0.61$, $p < 0.0001$, filled circles), as well as when calculated for the population of all cells (Pearson $R = 0.40$, $p < 0.0001$).

When the network was trained using a subset of trials in which a color cue was presented and then tested using the remaining color cue trials, the linear estimator performed well (>95% correct). The network also performed well when trained using a subset of mixed color and shape cue trials and then tested using the remaining trials. When trained on color cue trials but tested on shape cue trials, the network performed at only slightly above chance level (57%). However, when we restricted the data to cells that had been classified as rule selective by the ANOVA, performance rose to well above chance (73% correct). This indicates that, during the delay period, task-specific information can be extracted from a subset of cells. It is important to note that training the network on responses obtained from one task instruction cue set enabled the network to classify responses obtained using the untrained task instruction cue set. This confirms that some neurons encode information about particular tasks and are not merely responding to the sensory features of particular cues. However, cue effects overwhelm task-specific information when the entire population of neurons is considered.

Next, we hypothesized that cue effects would diminish and task-specific information would become more prominent with time. To test this, we trained a second network on data recorded late in color cue trials, just after the stimulus was presented. Once trained, the network was tested using data from (untrained) shape cue trials. This time, performance was well above chance (72% correct), even when data from all neurons were included in the network. Similar results were obtained when the network was trained on shape cue trials and tested on color cue trials. Once again, the fact that a simple network trained using data from one task instruction cue set could correctly extract task rule information on trials using an untrained task instruction cue set demonstrates that task-specific information is reliably encoded by populations of neurons in PPC.

Since the PPC includes many neurons whose firing is known to be related to overt saccadic eye movements (Synder et al., 1997) and to spatial attention (Colby and Goldberg, 1999; Bisley and Goldberg, 2003), we wished to rule out the possibility that task-selective responses reflect an oculomotor or attentional strategy. An example of a potential oculomotor strategy would be to direct gaze to different sections of the screen in the different task conditions. In order to discourage such a strategy, we randomly jittered the position of each stimulus, such that the monkeys could not predict where the stimuli would appear. An alternative approach would have been to require that the animals maintain central fixation throughout the memory period. This approach would have the disadvantage that, if fixation were enforced, animals might then adopt a strategy of covertly allocating their attention to different locations in the two different task conditions. We were able to rule out the differential allocation of attention by allowing the animals to move their eyes at will and observing no systematic differences in eye movements or eye position.

Visual inspection of the eye movement traces confirmed that the animals did not systematically redirect their gaze before the stimuli appeared (Figure 4). Monkeys typically maintained fixation at screen center until the stimulus appeared, despite not being required to do so. On average, animals made only one saccade in the late delay period per 5.02 trials. Once the stimulus appeared, animals showed a normal pattern of eye-hand coordination and made a saccade to the left or right button shortly before reaching for it.

To test for an effect of saccades producing a task-specific difference in neuronal activity, we determined the average eye position in the two task conditions during the late delay period for each neuron. There was a significant difference ($p < 0.05$) in average eye position

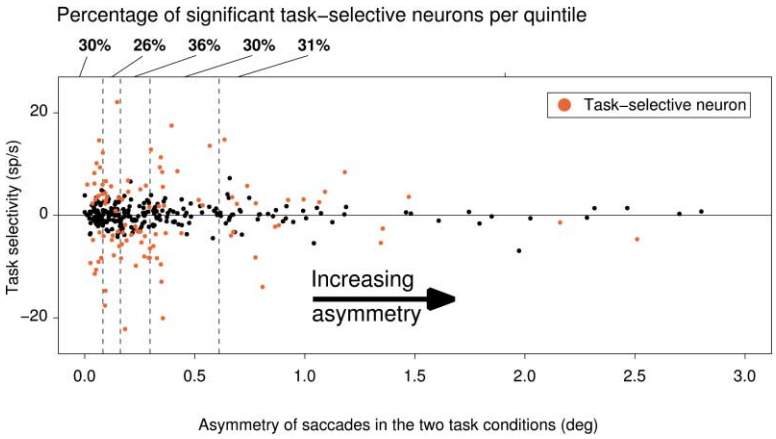

Figure 8. Plot of Saccadic Asymmetry in the Two Task Conditions against Task Selectivity

Saccadic asymmetry was calculated as the vectoral difference in saccade amplitude obtained during the late delay periods of the two different task conditions. Cells were ranked and divided into quintiles based on the degree of saccadic asymmetry that occurred while the neural responses were being recorded. The percentage of cells with significantly different delay period activity under the two task conditions is shown for each quintile (top). Task-selective cells (red) are evenly distributed across the five quintiles (χ^2 test, $p > 0.8$).

between the two task conditions in only 7% of task-selective neurons. Across all cells, there was no significant relationship between the difference in eye position and the magnitude of task selectivity (Pearson $R = -0.02$, $p > 0.8$). We found similar results for a range of other intervals, spanning times both before and after target appearance.

To test for an effect of saccades on neuronal firing rate, we determined the difference in the endpoints of saccades made during the late delay periods of the two task conditions. Figure 8 shows this difference for each cell against the difference in firing rate under the two task conditions. To test the hypothesis that asymmetries in saccades under the two task conditions are responsible for differences in cell firing, we divided the cells into quintiles based on how asymmetric the animal's saccadic behavior was while the neural data was being collected. If differences in saccades drive the differences in firing, then the percentage of task cells should be higher in the more asymmetric quintiles. Instead, we found that the percentages of task-selective cells in the quintiles were not significantly different from each other (χ^2 test, $p > 0.8$). This is further evidence that task selectivity and eye movements are not related.

Finally, for each task-selective cell, we compared the direction of saccades made during the late delay period in the task conditions using Watson's two-sample test of homogeneity (Jammalamadaka and Sengupta, 2001). Only 10% of task-selective cells showed a significant difference (α level of 0.05) in saccade direction. Thus, systematic differences in eye position, saccade direction, or saccade amplitude cannot explain the effects observed in this study.

Discussion

We have presented evidence that a subset of neurons in the PPC, concentrated in the lateral bank of the intraparietal sulcus and on the adjacent angular gyrus, responds selectively to cues for different task rules. While some of this activity merely reflects sensory properties of the cue used to instruct the particular task, a small but significant component of the activity reflects an abstract signal related to the identity of the upcoming task. We suggest that this signal is likely to play a role in task preparation (Stoet and Snyder, 2003b) and therefore can be considered a neural correlate of cognitive set (Nakahara et al., 2002). In particular, we have demonstrated that this selectivity for one task over another does not reflect either overt or covert differences in spatial orientation and therefore cannot be ascribed to spatial attention (Colby and Goldberg, 1999; Bisley and Goldberg, 2003; Kusunoki et al., 2002; Wardak et al., 2004). Finally, signals related to motor set or motor intention, although known to be present in this part of the PPC (Calton et al., 2002; Dickinson et al., 2003; Snyder et al., 1997), would not be expected to be different for the two task conditions, since the motor responses that can be prepared during the delay period are common to both tasks (e.g., lift the paw off the home key).

The encoding of cognitive set is closely related to executive control, working memory, and attention. The first two functions are often considered to be the domain of the frontal cortex (White and Wise, 1999; Asaad et al., 2000; Tanji and Hoshi, 2001; Wallis et al., 2001), while the posterior parietal cortex is seen as providing an attentional filter that operates on incoming stimuli, boosting those stimulus-driven signals that are task relevant and suppressing those that are task irrelevant (Corbetta and Shulman, 2002; Chawla et al., 1999). Cognitive set is closely related to attentional modulations. However, in the current study, we report modulations that occur *before* the presentation of the stimulus, while the animal is viewing a blank screen. The term "attentional modulation" is most often used to describe a modulation that *follows* stimulus presentation. An exception to this occurs for spatial attention: attentional modulations have been described which *precede* stimulus presentation (Luck et al., 1997; Ferrera et al., 1994). However, in our study it is unlikely that animals attended to different spatial locations during the delay period, since there were no asymmetries in the animals' overt eye movements, which were unconstrained (Figures 4 and 8).

Chawla et al. (1999) describe task-selective modulations of activity in human parietal cortex as an anticipatory effect of attention. These modulations occurred in the presence of a random dot pattern stimulus and therefore may have been stimulus evoked, not anticipatory. This objection aside, the term "anticipatory effect of attention" adequately describes the phenomenon we

have observed. However, this term may suggest that parietal cortex is the site at which these effects appear, but not the source. In fact, very few experiments, and certainly not the current experiment, address this issue. Therefore, while recognizing that the distinction is primarily semantic, we prefer the more neutral term "cognitive set" (White and Wise, 1999; Nakahara et al., 2002) over "anticipatory attentional modulation" to describe our findings.

While the term cognitive set has been most often applied to neural activity in frontal areas, including, for example, the prefrontal cortex (Nakahara et al., 2002; Konishi et al., 2002) and premotor cortex (Wallis and Miller, 2003), there have been many reports of task-specific modulation in the posterior parietal cortex, starting with the classic study of Bushnell et al. (1981). Until recently, however, it appeared that parietal task-specific modulations encode task-relevant sensory information (Assad, 2003) and not abstract signals related to task preparation and therefore do not qualify as cognitive set signals. Many studies have shown neural correlates of spatial location or motion that are modulated by task contingencies (Cohen and Andersen, 2002; DeYoe and Van Essen, 1988; Colby and Goldberg, 1999; Bisley and Goldberg, 2003; Snyder et al., 1997, 2000; Goldberg et al., 2002; Kusunoki et al., 2002; Treue and Maunsell, 1996; Britten et al., 1996). Other studies have shown task-specific encoding of nonspatial stimulus features (Toth and Assad, 2002; Sereno and Maunsell, 1998; Sawamura et al., 2002). In each case, task-related modulations encode concrete sensory information, not abstract signals related to task preparation. For example, in a study by Toth and Assad (2002), spatial targets were color coded, and the animals were trained either to make saccades toward the targets irrespective of color or to make saccades on the basis of target color irrespective of target location. Cells weakly coded target color on trials in which color was relevant. However, when the mapping rule between color and saccade direction was reversed, color coding was maintained, suggesting that these cells encode sensory properties and not the rule.

Calton et al. (2002) and Dickinson et al. (2003) took a step away from featural encoding by showing that cells in the parietal reach region and LIP are modulated based on whether an animal plans a reach or a saccade. This modulation was entirely independent of spatial information, since at the time of the modulation, the spatial goal of the movement was unknown. However, once again this modulation was encoding a concrete variable, namely, the effector that the animal was planning on moving. This is different from an encoding of cognitive set, in which representations are independent of specific stimuli or specific responses.

Brain imaging studies in humans have also found that cognitive set signals are prominent in the parietal cortex, although these findings are often given less emphasis than similar findings from the frontal cortex. Like the nonhuman primates in the current study, humans performing a task-switching paradigm show clear set-related activations in PPC (Sohn et al., 2000; Gurd et al., 2002, 2003; Dove et al., 2000; Le et al., 1998; Kimberg et al., 2000; Rushworth et al., 2001; Luks et al., 2002; Moll et al., 2002; Braver et al., 2003; Dreher et al., 2002; Sylvester et al., 2003). Other studies using different paradigms have arrived at similar conclusions. For example, when subjects are cued in advance to look for a particular direction of motion in an upcoming visual display, set-related activity is maintained in the parietal cortex or in the parietal and frontal cortices (Shulman et al., 1999, 2002; Hopfinger et al., 2000). Thus, there is strong evidence that parietal cortex encodes set-related signals in both human and nonhuman primates. It is not known whether this signal originates in the parietal cortex or whether it merely reflects a control signal elaborated in the frontal cortex. This question might be resolved by looking at the relative timing of set-related activity in the two cortices, although the difference is bound to be small. In fact, it is quite possible that neurons in diverse locations are linked together to form a single functional network, such that set-related signals evolve simultaneously in multiple locations. In any case, however, our data provide clear evidence of abstract signals related to task preparation in the posterior parietal cortex of the monkey.

Experimental Procedures

We recorded single neurons from two male rhesus monkeys (*Macaca mulatta*), using tungsten microelectrodes (FHC, Bowdoinham, ME) inserted through a grid with 1 mm spacing (Crist Instrument, Hagerstown, MD). Recording chambers were attached flush to the skull at 8 mm P, 12 mm L (Horsley-Clarke coordinates). Data were recorded from all isolated neurons but were discarded if the monkey performed at less than 75% correct on trials for which stimuli required opposite responses in the two tasks. (Complete disregard of the task cue would result in a success rate of 50% on these trials.) After chamber implantation, we used MRI to localize the recording sites in each monkey (Figure 2). Data were processed using the software packages Caret and SureFit (Van Essen et al., [2001], http://brainmap.wustl.edu/caret). Areal boundaries were based on Lewis and Van Essen (2000) (http://brainmap.wustl.edu:8081/sums/archivelist.do?archive id=568272).

Animals were seated in a sound-attenuating dark room facing a touch-sensitive screen (30 × 20 cm) at a distance of 25 cm. Animals performed between 1500 and 3000 trials per experimental session. Trial order was randomized and balanced across experimental conditions. Eye movements were recorded using a scleral search coil. Trials began with animals contacting a key (Efector, Inc.) positioned 2 cm below the screen. Two white squares in the bottom left and right corners of the touch-sensitive screen functioned as response buttons and were visible throughout the entire trial. Task cues were presented by setting the screen color to yellow or blue or by displaying an upright or inverted white equilateral triangle (14.7°) at screen center for a 250 ms period (Figure 1). For monkey 2, stimuli were colored bars (6.9° × 0.7°) oriented within 10° of either horizontal or vertical, located at a random location within 5° of screen center. Bar color was randomly chosen from many shades of red and green (e.g., pink, orange, cyan). The many combinations of colors and orientations were intended to encourage the use of general rules rather than a "lookup table" strategy for solving the tasks. We used a slightly different stimulus for monkey 1. The differences are described fully in the Supplemental Data (available at http://www.neuron.org/cgi/content/full/42/6/1003/DC1) and in previous publications (Stoet and Snyder, 2003a, 2003b). Briefly, we used squares (13.6°) with a luminance contrast between the inside and the outside border instead of lines. The inside and outside border each comprised half of the total surface of the stimulus. Target color and brightness levels were randomly varied to produce a set of 104 different stimuli. The differences in the stimuli used for the two monkeys may have produced subtle differences in the results. However, the fact that the basic findings were consistent between animals helps to establish the generality of our conclusions.

The delay period was kept constant within each session. For purposes not related to the current study we used different delay

periods during different sessions. Most data were collected using a period of at least 400 ms. Animals were not required to fixate during this period (see Results for evidence that neither overt eye movements nor covert shifts of attention can explain our results).

Only data from correct trials were analyzed. We determined task selectivity by testing the difference in mean spike rate between the two task conditions. For data collected using one task instruction cue set, task selectivity of each neuron was defined as a significant difference in firing rate in the late delay period, that is, 150–250 ms (depending on the delay interval used during recording) before stimulus onset (Student's t test, α level of 0.05). For neural data collected with both task instruction cue sets, task selectivity was defined as a significant main effect of task in a two-factorial ANOVA with factors task rule (color and orientation task) and task instruction cue set (colors or shapes) in the 250 ms delay before stimulus onset. Directional selectivity was defined as a significant difference in firing rate in the 200 ms preceding response onset (as tested with Student's t test, α level of 0.05).

The linear estimators were modeled with the NNET library of the statistical software package R (Venables and Ripley, 2002). We set the values of input nodes to the spike activity, recorded during 5000 randomly chosen trials, in either the 250 ms before stimulus onset or the 250 ms following stimulus onset. Initial connection weights were randomized values ranging between -0.1 and $+0.1$. The network weights were fitted using a gradient descent algorithm.

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